# THE WINGS OF INSECTS.

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## CHAPTER IV (*continued*).

### *The Specialization of Wings by Addition.*

#### IV. THE VENATION OF THE WINGS OF EPHEMERIDA.

THE determination of the homologies of the wing-veins of May-flies appears, at first sight, to be an extremely difficult problem; for the wings of these insects are very different from those of any other order. But, as soon as one understands the ways in which the wings have been modified, it is easy to identify the principal veins.

In this order a marked cephalization of the flight function has taken place, which has resulted in a great reduction of the hind wings of all living forms. In some cases (*Cænis et al.*) this has gone so far that the hind wings are wanting.

In a few genera (*Oligoneura et al.*) both pairs of wings are furnished with but few veins. It requires only a little study, however, to convince one that these genera with few-veined wings are degraded and not generalized. It is in the fore wings of those forms in which many wing-veins have been retained that the homologies of the wing-veins are most easily determined.

Fig. 69 represents the venation of a species which will serve well as a type of the recent May-flies; and the lettering of the figure indicates our conclusions regarding the homologies of the veins. But the most characteristic feature of the wings is not shown in the figure. If the reader will examine one of the larger May-flies, he will see that the corrugation of the wings is much more perfect than in any other order of insects, extending to all parts of the wings.

This fan-like structure of the ephemerid wings has been referred to by many writers. But it is worth while to point

out in this place the degree of perfection that has been reached in the alternation of convex and concave veins. In the accompanying table the names of the convex veins, those veins that follow the crests of ridges, are printed in Italics; while the names of concave veins, those veins that follow the furrows, are printed in Roman type.

Table of Wing-Veins of Ephemerida.

| | | | | |
|---|---|---|---|---|
| *C.* | *Costa* | | | *C.* |
| Sc. | Subcosta | | | Sc. |
| *R.* | *Radius* | | | $R_1$ |
| Rs. | Radial sector | Vein $\mathrm{R}_{2+3}$ | Vein $\mathrm{R}_2$ | $\mathrm{R}_2$ |
| | | | *Vein* $R_3$ | $R_3$ |
| | | Chief accessory radial vein | | 1 |
| | | Vein $\mathrm{R}_{4+5}$ | *Vein* $R_4$ | $R_4$ |
| | | | Vein $\mathrm{R}_5$ | $\mathrm{R}_5$ |
| *M.* | *Media* | *Vein* $M_{1+2}$ | *Vein* $M_1$ | $M_1$ |
| | | | Vein $\mathrm{M}_2$ | $\mathrm{M}_2$ |
| | | *Vein* $M_3$ | | $M_3$ |
| Cu. | Cubitus | Vein $\mathrm{Cu}_1$ | | $\mathrm{Cu}_1$ |
| | | *Chief accessory cubital vein* | | *1* |
| | | Vein $\mathrm{Cu}_2$ | | $\mathrm{Cu}_2$ |
| *1st A.* | *1st Anal vein* | | | *1st A.* |
| 2d A. | 2d Anal vein | | | 2d A. |
| *3d A.* | *3d Anal vein* | | | *3d A.* |

One of the most characteristic features in the venation of the wings of May-flies is that the radial sector plays the part of a principal vein; it originates near the base of the wing; and, as a rule, it is detached, in the adult, from the main stem of the radius.[1] For this reason it is given the position of a principal vein in the table.

If this modification be made, it will be seen that, when the principal veins are considered, there is a strict alternation of convex and concave veins; and that in the case of the forked veins (the radial sector, the media, and the cubitus) the principal branches of a vein are of the same nature as the main stem.

It will also be seen that this alternation of convex and concave veins exists in the distal portion of the wing. In those

[1] In certain Plecoptera and Trichoptera the radial sector of the hind wings is detached in a similar manner.

cases where a vein has an even number of branches (the radial sector and the cubitus) the alternation has been attained by the development of an accessory vein. These are indicated in the table as chief accessory veins, and are lettered I in the figure. Many other accessory veins are developed at the margin of the wing in a more or less irregular manner; but whenever a second accessory vein extends far into the disk of the wing it is accompanied by a third, one being convex, the other concave. The anal area of the wing, where the accessory veins are more of the nature of braces, like cross-veins, is not included in this statement, nor in that which follows.

Correlated with the development of a triangular form of wing, which involves an expanding of its outer margin, is the fact that the accessory longitudinal veins are all added distally in the May-flies. But the method of development of these veins appears to be radically different from what it is in the Neuroptera.[1] There the accessory longitudinal veins are preceded by tracheæ, which arise as fine twigs at the tips of older tracheæ, and which in the course of phylogenetic development branch off from the parent tracheæ farther and farther from the margin of the wing, thus making room for the development of other twigs. Here, in the May-flies, the accessory longitudinal veins are evidently thickened folds, which arise more or less nearly midway between other veins. A similar thickening of a fold occurs in the Diptera, where, in certain Asilidæ, the anal furrow is vein-like in structure.

A fact of prime importance in the study of the homologies of the wing-veins of May-flies is that the corrugations of the wing are the most persistent features of it. Hence the most important criterion for determining the homology of a vein is whether it is a concave or a convex one. The basal connections of the veins are very inconstant, and are often misleading. We have already referred to the separation of the radial sector from the main stem of the radius in the adult (its true origin is easily seen when the tracheation of the wings of certain nymphs is studied); and other separations and secondary attachments are common. A good illustration is furnished by the wings

[1] See *American Naturalist*, vol. xxxii, pp. 771, 772.

represented by Fig. 69. In the hind wing, vein $Cu_2$ is apparently a branch of the first anal vein (marked $A$ in the figure); but in the fore wing, which is less modified, its primitive connection is preserved; although even here a prominent bend has brought it near to the anal vein, and only a step more would be required, the fading out of the basal section, to reach

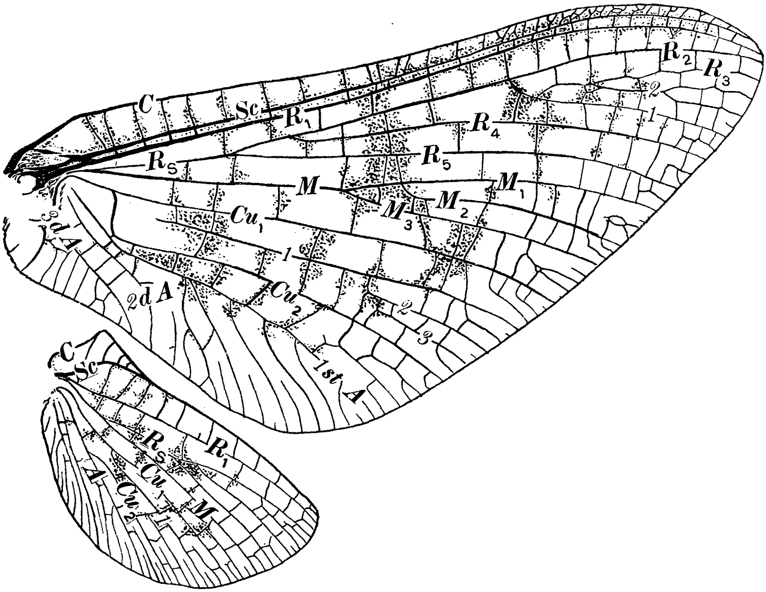


FIG. 69. — Wings of *Ephemera.*

the condition attained in the hind wing. But the concave nature of this vein in the hind wing indicates its homology in spite of its misleading basal connection.

It should be remembered that the convex or concave nature of a vein is the result of a corrugation of the wing and not the cause of this corrugation. The theory of Adolph that the two sets of veins have a different ontogenetic development has absolutely no foundation in fact, as will be seen when we come to study the development of wing-veins, and as was suspected by Brauer and Redtenbacher.[1]

The primitive insect wing was doubtless flat. It makes no

[1] *Zoologischer Anzeiger*, 1888, p. 443.

difference, so far as this point is concerned, whether we believe that the wing is a modified tracheal gill or a transformed parachute-like expansion of the body wall. In either case it is highly improbable that it was fanlike at first. It was not until the wing became an organ of flight that a corrugation of it was beneficial; and even then this corrugation did not spring into existence suddenly, only to be lost in most of the orders of insects; as must be inferred, if we accept the theory of Adolph, that the wing of a May-fly represents the primitive type of this organ.

The stiffening of the costal margin of the wing by the formation of a subcostal furrow has been attained in most of the orders of insects; and in several of them the formation of folds has extended, to a greater or less degree, to other parts of the wing. But, as a rule, this method of specialization has not been the most important one in perfecting the wing. In the Odonata it has been carried farther than elsewhere, among living insects, except in the Ephemerida. But in the Odonata it has been supplemented by other methods of specialization, already discussed, with the result that an exceedingly efficient organ of flight has been developed in that order; while in the Ephemerids the cephalization of the flight function and the corrugating of the wings have been the chief lines along which specialization has extended. The former has doubtless added much to the efficiency of the wings; but a too close adherence to the latter method of specialization has resulted in the formation of a rather indifferent organ; although it is the most perfect development of its peculiar type.

We have studied the tracheation of many nymphs of May-flies, but with results much less satisfactory than those we have reached in the study of other orders of insects with many-veined wings. In all nymphs of May-flies that we have examined, a greater or less reduction of the tracheæ appears to have taken place; and in many of them a large proportion of the longitudinal veins contain no tracheæ. And, too, the presence or absence of a trachea in a vein appears to have little significance. As an example of this the wings of two nymphs are before the writer, in which the venation is so similar that there

is not the slightest difficulty in tracing the homologies of the veins. In one the radial sector and the media contain well-preserved tracheæ; in the other there is not the slightest trace of a trachea in these veins. On the other hand, in the latter the cubital trachea is forked, one of the branches traversing vein $Cu_2$; while in the former the cubital trachea is simple, there being not the slightest indication of a trachea in vein $Cu_2$.

The basal connections of the trachea of the wing are very different from what we have seen elsewhere. In the Plecoptera there are two distinct groups of tracheæ which enter the wing;[1] the same is true of certain cockroaches;[2] in all other forms

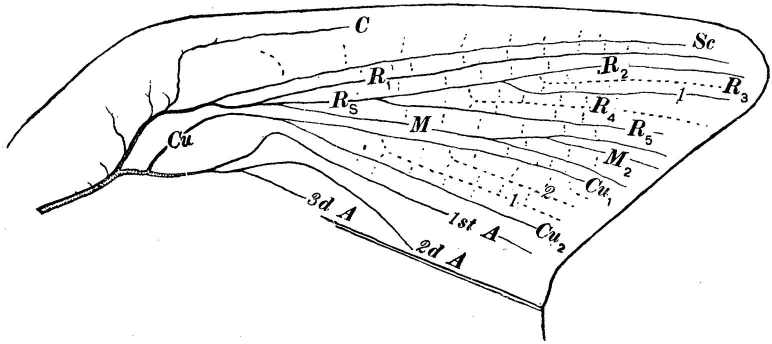


FIG. 70.—The tracheation of a wing of a May-fly nymph.

that we have studied, except the May-flies, a transverse basal trachea connects these two groups, and from this transverse trachea (transverse in relation to the wing, but longitudinal in relation to the body) the principal tracheæ of the wing extend more or less nearly at right angles to it.[3] In the May-flies a single trachea arises from the principal longitudinal trachea of one side of the thorax, and, after giving off a branch to the corresponding leg, passes directly to the base of the wing. Here it divides into several branches which continue in approximately the same direction and become the principal tracheæ of the wing.

In some cases this trachea extends into the wing before it divides. But in other forms, which we regard as more general-

[1] *American Naturalist*, vol. xxxii, p. 238, Fig. 8; p. 239, Fig. 9.
[2] *Loc. cit.*, p. 773, Fig. 56. [3] *Loc. cit.*, p. 772, Fig. 54.

ized, it separates into two trunks in the thorax near the base of the wing (Fig. 70); from one of these arises the costo-radial group of tracheæ, and from the other the cubito-anal group.

Fig. 70 will serve to illustrate what may be considered the type of tracheation of the wings in this order. It was made from a study of the nymphs referred to above. The positions of those longitudinal veins that contained no tracheæ in these nymphs are indicated by dotted lines.

The discussion of the venation of the wings of Ephemerida brings up the question of the venation of the primitive insect wing. For, in several of the more important papers on the homologies of wing-veins, it has been assumed that the wings of May-flies resemble closely the wings of the primitive winged insect.

The great preponderance of the many-veined type among the insect wings that have been found in the Carboniferous rocks has doubtless strengthened the quite generally accepted view that the primitive winged insect had many wing-veins. Thus Redtenbacher states:[1]

> The geologically older Orthoptera and Neuroptera show a much richer venation than the Coleoptera, Lepidoptera, Hymenoptera, and Diptera; likewise among the Rhyncota, the oldest forms, the Cicadas and the Fulgoridæ, possess much more numerous veins than the Hemiptera. There is apparently, then, no doubt that the oldest insect forms were provided, to a certain extent, with a superfluity of veins, and that, in the course of development, all the superfluous veins disappeared by reduction, and in this way a simple system of venation was brought about.

But we have shown that all the existing types of insect wings can be derived from one in which there are but few wing-veins — our hypothetical type, already figured several times. The deviations from this type in the more generalized members of the greater number of the orders of insects is slight. And we have pointed out the ways in which it is being modified, on the one hand by the coalescence of veins, and on the other by the development of accessory veins. While this is easy to understand, it is very difficult to conceive how the wings of the Lepidoptera, Diptera, and Hymenoptera could have been

[1] *Annalen des k. k. nat. Hofmuseums*, Bd. i, p. 153.

evolved from a wing of either the ephemerid or neuropterous type. After a wing had been strengthened by many cross-veins, it is not probable that these should disappear with the exception of the few to which we have applied names[1] in so many different orders, in so nearly an identical manner. Forms with reduced venation occur in most of the orders, but the results of these independent reductions differ greatly from each other. It is necessary, therefore, to examine again the paleontological evidence.

The great preponderance of many-veined wings in the Carboniferous rocks is probably due to the fact that doubtless then, as now, insects with many wing-veins were the ones that lived near water, and were, therefore, the ones most likely to be preserved as fossils.

Another point which should be taken into account is that, notwithstanding the great antiquity of the Carboniferous times, it was a comparatively late period in the history of insects, for winged insects appeared in the Silurian. We are carrying our investigations back only a step, although it is a long one, towards the period when wings were first developed by studying Carboniferous fossils.

Unfortunately, our knowledge of Silurian insects is meager. Moberg has figured an insect from the upper part of the lower Silurian; and Brongniart has figured and described a wing from the middle Silurian sandstone of Calvados, France. This we believe is all that is known regarding the insect fauna of the Silurian; and when we take into account the immensity of the period of time occupied by the deposition of the Silurian rocks, we are forced to admit that we know almost nothing regarding the older insects.

Of the Devonian insects, the remains of several are known. Those which are best preserved are *Homothetus fossilis* (Fig. 71), *Xenoneura antiquorum* (Fig. 72), and *Platephemera antiqua* (Fig. 73). (The figures given here are reproduced from Plate VII of Mr. Scudder's *Pretertiary Insects*.) A glance at these figures will convince the reader that the insects of the Devonian times varied greatly in the structure of their wings. For

[1] *American Naturalist*, vol. xxxii, pp. 233, 234.

these three insects differ as much from each other as do the more generalized members of widely separated orders of living insects. Evidently, comparatively high specializations in widely

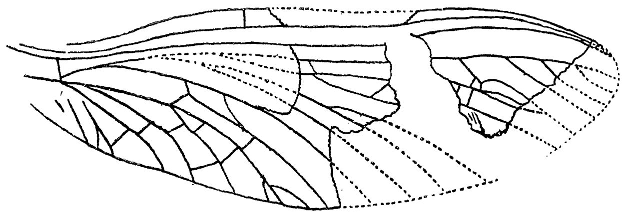

FIG. 71. — *Homothetus fossilis.*

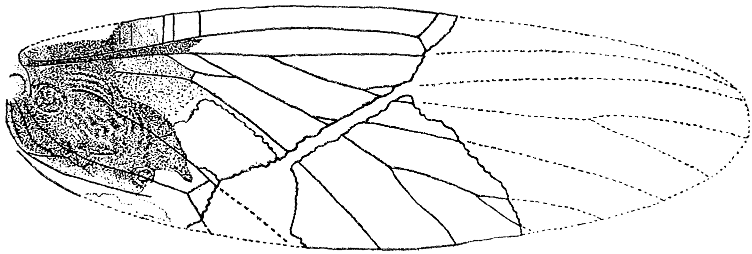

FIG. 72. — *Xenoneura antiquorum.*

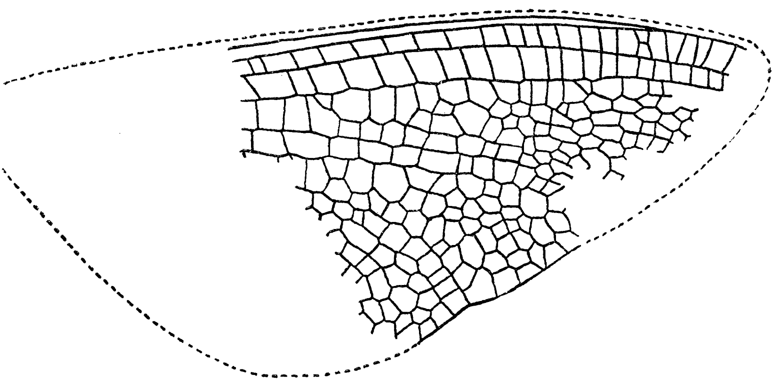

FIG. 73. — *Platephemera antiqua.*

different directions had been attained already at that early time. But the point to which we wish to call especial attention is that, of the three better-preserved Devonian insects, one (*Xenoneura*) had but few wing-veins. And when we consider the

slight amount of data that we have, the numerical preponderance of the many-veined type has no significance.

It is easy to conceive of the development of the wings of all living insects from forms allied to *Xenoneura*, by the different methods of specialization which we have pointed out; for it will be seen that the wing of this insect closely resembles our hypothetical type. And we can say, therefore, that the paleontological evidence does not contradict the conclusions drawn from a study of the ontogeny of living forms.